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AN ECOLOGICAL STUDY OF THE FLOOR FAUNA OF THE PANAMA RAIN FOREST

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AN ECOLOGICAL STUDY OF THE FLOOR FAUNA OF THE PANAMA RAIN FOREST*

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INTRODUCTION

The several parts of a biotic community must be studied intensively before the ecology of the entire community can be understood. Inasmuch as the floor stratum is an important component of a forest community, it was felt that a quantitative faunal study of this stratum coupled with an analysis of the environmental factors would yield results which would be a definite addition to our knowledge of the tropical rain forest.

The only comprehensive study of the surface fauna in the tropics known to the author is that of Dammerman (1925, 1937). The main object of this work was the determination of the number of species present on a given area. This research was carried out in various islands of the East Indies. Dammerman's method of collection was mainly a careful sorting out of the animals from the debris on one square meter. He treated a few samples in a Berlese Funnel. The samples sorted by hand ran about 120 individuals per square meter, but these figures are low because exact counts were not made of species which were represented by many specimens. The samples which were treated by the Berlese method yielded about 700 individuals per square meter. There was an average of 25 species for each square meter with a maximum of 88 species and a minimum of 4. A peak in number, both of species and individuals, was reached at the height of the rainy season. Beebe (1916) collected the material from four square feet in the Brazilian rain forest and examined it while en route to New York. Ants comprised 30 per cent of the total collections. The results for Acarina and Collembola were low,

*Contribution from the Zoological Laboratories of Northwestern University.

mainly because his technique would not yield good results for such minute forms. In all, he found 500 specimens and estimated that there were at least twice as many which had not been collected. On this basis there were about 4,000 animals per square meter.

A fairly substantial body of literature has been built up concerning the fauna of the soil and its surface. These various investigations fall into two main categories, qualitative and quantitative. Although much of the earlier work dealt with the obvious question of what kinds of animals inhabit the soil and surface debris, in more recent years methods were gradually perfected for determining the number of animals in this stratum. It is not possible here to give a complete review of the literature but a bibliography is included in which a large portion of the pertinent material is cited.

The collections upon which this study is based were made on Barro Colorado Island, Gatun Lake, Panama Canal Zone, during July and August of 1938. This island was formed in 1914 when the Gatun Dam backed up the waters of the Chagres River to make Gatun Lake, the central portion of the Panama Canal. The higher regions of the former valley were left as islands in the lake, Barro Colorado being the largest one. The greatest length and width of the island are approximately 3 miles, and the area is 6.64 square miles. Due to irregularities, the shore line is over 40 miles long. The highest point on the island is 537 feet above sea level, 452 feet above Gatun Lake.

The annual rainfall (1926-1930) was 100.10 inches, 7.06 inches of which fell in the first four months of the year. With rare exceptions the temperature ranges from 70 degrees to 90 degrees Fahrenheit. The mean daily temperature remains practically the same from month to month, while the daily range varies from 5 to 15 degrees Fahrenheit. Relative humidity fluctuates between 77 per cent in the dry season and 88 per cent in June, July, and August. The above description is based, in part, on that given by Enders (1935).

In regard to the forest itself, Enders quotes Kenoyer (1929, p. 201) as follows: "About half of it (the forest covering the island), that farthest from the Canal, is apparently primeval forest, although Standley (1927) points out that in a region which has been for over 400 years an important trade route it is difficult to prove that a given tract of land has not at some time been cleared and put under cultivation. The other half is occupied mainly by secondary forest, the largest trees of which scarcely exceed a foot in diameter at the base. Apparently it has become forested from a cleared condition of about fifty years ago." Enders prepared a map, showing the areas considered to be primeval and those which are

second growth. Most of the samples taken in the course of this study were from areas represented by Enders as primeval forest.

The specific portion of the habitat with which we are here concerned is the forest floor. The lack of undergrowth in the rain forest is especially noticeable to one familiar with the northern deciduous forest. There are very few herbs and for the most part the ground is devoid of low-growing plants. The stratification typical of all forests is present in the tropical rain forest (Allee, 1926), but the first living plant stratum of any importance, passing from the ground upward, is that of the higher shrubs (to ten feet). The litter on the floor of the forest is made up of dead leaves, twigs and other plant products, and the feces and remains of animals.

MATERIALS AND METHODS

Eleven large quadrats, one meter square, were examined in the field. A frame which enclosed an area of exactly one square meter was placed on the ground and all of the living vegetation was removed and weighed. The forest floor litter was next carefully examined; each fallen leaf and twig was picked up and all animals that could be seen were removed. All of this debris was also weighed. The surface was completely cleared of the layer of molding plant material and the loose soil on the surface was examined. A complete survey of one square meter in this manner took about five or six hours.

Eighteen small quadrats, 25 cm. square, were also studied. A frame was placed on the ground and all of the material enclosed was put into an aluminum can and taken to the laboratory, where it was weighed and examined, a small portion at a time, in a large tin pan.

In the case of all of the large quadrats, and most of the small ones, a sample of the leaf mold close to the quadrat was taken to the laboratory and after being weighed it was treated by the Berlese method. The material was placed in a large funnel, at the small end of which was a fine screen. At the upper end of the funnel were set three 40 watt carbon filament bulbs in a triple socket. The heat from this source gradually dried out the leaf mold, driving the animals down to the small end of the funnel and out into a vial of alcohol. The samples were treated in the funnel for six or seven hours. A longer treatment would have been desirable, but the electric light unit in use on the island could only be operated between 5 P. M. and 1 A. M. Because of the high humidity, it was impossible to use the Berlese apparatus effectively without heat. Only one Berlese sample could be handled each day, so in those cases where two of the 25 cm. quadrats were investigated in one day, a

Berlese analysis was carried out for only one of them. The can in which the sample was carried was rinsed out with alcohol to get those forms which might have adhered to the sides.

Berlese samples were taken for ten of the eleven large quadrats and for thirteen of the eighteen small ones. In the analysis which follows, except as otherwise noted, all quantitative studies are based on quadrats which were studied by both Berlese and manual collections.

In arriving at a figure for the number of animals present on a given quadrat, the number taken in the manual collections was used for all groups except the Acarina and Collembola. For these forms, whose small size made it impossible to collect all present on a quadrat, the results obtained by the Berlese funnel were used. The sample treated in the funnel was, presumably, comparable to that in the larger portion examined in detail by hand. Assuming that practically all of the Acarina and Collembola were driven out of the funnel by the heat, we had a figure for the total number present. Using this figure as a basis, the number of Acarina and Collembola in the main sample was determined. For example, on quadrat S-1 there were 244 grams of leaf mold. The sample used in the Berlese funnel weighed 84 grams. There was 2.9 times as much material in the main sample, so the number in the Berlese sample multiplied by 2.9 gave the number of Collembola and Acarina which would have been obtained had the entire quadrat been treated in the Berlese funnel.

A soil sample was taken for each quadrat and subsequently analyzed.*

The quadrats were taken at random at various places on the Island. The majority of them were within three or four hundred meters of the main laboratory buildings.

Rainfall was recorded by an automatic rainfall gauge located near the laboratory. Soil and air temperatures were recorded at intervals during the collection of each quadrat.

The material collected from each quadrat was placed in a vial containing 70 per cent alcohol. The Berlese and manual collections were kept separate. Upon returning to the university the animals were sorted into various taxonomic groups, with the aid of a binocular dissecting microscope. Some of the animals were colorless, others were dark colored, and the material was sorted over both a light and a dark background so that none of these forms would be missed. The animals were each measured, the smaller ones with the aid of an ocular micrometer and the larger ones with a steel ruler.

* The analysis was made by Dr. R. H. Bray of the University of Illinois.

In order to have sound taxonomic determinations, material was sent to specialists in the various groups wherever possible. In some cases there was no one available who could make determinations and in others reports have not yet been received. As a result, in some groups the determinations are to species and in others merely to family or order. Because the Neotropical fauna is poorly known in many of the invertebrate groups in question, even those sent to specialists are not all determined to species.

RESULTS

ENVIRONMENTAL FACTORS

The rainfall was recorded by an automatic rainfall gauge of the tipping bucket type and the daily record for the duration of the collections is given in Table 1. Relative humidity records were taken with a Lambrecht Recording Hygrometer, and temperature records were taken with a Taylor Recording Thermograph. The results are given in Tables 2 and 3. A comparison of the temperature and relative humidity values for the clearing and forest shows the marked effect of the forest on these two factors. The temperature in the forest is lower in the daytime and higher at night while the relative humidity is higher in the daytime and somewhat lower at night.

A comparison of the wet and dry weights of the soil samples gives an index of the moisture content of the litter. This information, expressed as the percentage of moisture in the total weight, is given in Table 4.

During the collections of the one-meter quadrats, the soil and air temperatures were recorded at intervals. The data for these readings are presented in Table 5. The differences between soil and air temperatures in the forest are somewhat comparable to those in the forest and clearing. The soil temperature is lower in the daytime and higher at night than the air temperature.

The results from the analysis of the soil samples have been tabulated in Table 6. Dr. Bray reports, "In general these samples and their tests are typical of the highly organic covering of some forest soils; lots of available K, Mg, and Ca, and very little acidity and with the N and PO_4 tied up in the organic matter."

Table 1. Rainfall (in inches)

Date	Midnight to 6 A.M.	6 A.M. to Noon	Noon to 6 P.M.	6 P.M. to Midnight
July 1	0	0	.01	0
2	0	0	.17	0
3	0	0	.15	.28
4	.01	.01	.08	0
5	1.05	0	0	0
6	0	0	.32	.02
7	0	0	.58	.02
8	0	0	0	0
9	0	0	.05	.06
10	0	0	.20	.02
11	0	0	.35	0.
12	0	0	0	1.41
13	.01	.03	.27	.21
14	0	.04	.05	0
15	.01	0	.10	0
16	.02	0	.19	0
17	0	.21	.29	0
18	0	.01	.53	0
19	.03	.01	0	.05
20	0	0	0	.03
21	.01	.01	0	.02
22	0	0	.41	.13
23	.28	0	.12	.40
24	0	.05	.09	0
25	.01	.11	.54	0
26	.01	.01	0	0
27	0	.08	.26	.01
28	0	0	0	0
29	.06	0	0	0
30	0	0	0	.02
31	0	0	1.35	0
Aug. 1	0	0	0	0
2	0	0	.25	.12
3	.05	0	0	.08
4	0	0	.73	.05
5	.47	.01	0	.18
6	.01	0	.01	.11
7	.08	0	.56	.04
8	0	.01	.15	.41
9	0	0	.22	.09
10	.04	.01	1.70	.31

Table 2. Relative Humidity (in per cent)

Clearing

Time	July 11	July 12	July 13	July 14	July 15	July 16	July 17
6 A.M.		96	100	100	100	100	100
12 Noon		76	80	80	78	76	80
6 P.M.	90	94	100	100	96	96	96
12 Mid.	96	100	100	100	100	100	100

Forest

Time	July 25	July 26	July 27	July 28	July 29	July 30	July 31
6 A.M.		98	96	97	97	97	98
12 Noon		96	96	98	97	98	98
6 P.M.	98	94	96	96	96	97	96
12 Mid.	98	96	98	98	96	97	97

Table 3. Temperature (degrees Fahrenheit)

Clearing

Time	July 11	July 12	July 13	July 14	July 15	July 16	July 17
6 A.M.		76	77	76	76	78	78
12 Noon		86	86	86	84	88	88
6 P.M.	78	82	76	78	78	78	78
12 Mid.	77	77	76	76	78	78	78

Forest

Time	July 25	July 26	July 27	July 28	July 29	July 30	July 31
6 A.M.		76	76	75	76	75	75
12 Noon		78	78	78	78	77	78
6 P.M.	78	78	76	78	77	77	78
12 Mid.	76	76	76	77	76	76	76

Table 4. Soil Moisture

Small Quadrats		Large Quadrats	
Quadrat No.	*Percentage H_2O*	*Quadrat No.*	*Percentage H_2O*
S- 8	52	2	44
S-10	64	3	41
S-12	56	4	33
S-13	65	7	48
S-15	56	8	51
S-16	54	9	48
S-17	46	10	68
S-18	41	11	69

Table 5. Soil and Air Temperatures in the Forest

Date		9 AM	10 AM	11 AM	12 N	1 PM	2 PM	3 PM	4 PM
July 9	Soil	75	76	76	76	76.5	76		
	Air	76.5	77	78	80	80	79.7		
July 12	Soil	77.5	77.5	77.5	77.5	78	78	78	76
	Air	79	79	79	79	80.2	79	79	78
July 13	Soil		74.8	76	76.5	75.8	75.8	76	76
	Air		76.5	78	78	74	74	73.5	73.5
July 14	Soil		77	77	77	77	77	77	
	Air		78	78.5	80.5	80	80.5	79	
July 15	Soil	77	77	77	77	77	77.5	77	
	Air	77	77.5	78.5	80	79	79.5	77	
July 17	Soil	77	77	77	77	77.5	78	78	78
	Air	78.5	79	79.2	80	80	81	81	76.5
July 18	Soil	77	76	76	76.8	76.8	76.8	76	76
	Air	76.5	77	78.3	78.2	78	76.8	76.5	76.5
July 19	Soil	78	78	78	77.5	78	78	77.5	77
	Air	77	78	74	74	75.5	76.5	77	77
July 31	Soil	77	77	77	77	77	78	78	78
	Air	76	76.5	77	79	80	80	79.6	79
Average	Soil	76.9	75.7	76.8	76.9	77	77.2	77.2	76.8
	Air	77.2	77.6	78.8	78.7	78.5	78.6	77.8	76.7

Table 6. Soil Analysis

Quadrat	K ppm*	NO_3 ppm*	Mg	Ca ppm*	SO_4	PO_4	pH	NH_3 ppm*
1	300	1	Slight	500	0	Low	6.4	
2	300	1	Medium	475	0	Low	6.4	
3	350	0	High	375	0	Low	5.8	
4	175	0	Slight	400	0	Low	4.8	
5	500	0	High	500	0	Low	5.8	
6	325	0	High	500	0	Low	6.6	
7	750	2	High	500	0	Low	7.0	
8	800	0	High	500	0		6.0	
9	575	0	High	500	0	Low	4.7	
10	750	2	High	500	0	Slight	7.8	
11	530	0	High	400	0	Low	7.0	
S-3	850	0	High	400	0	Low	5.5	
S-6	625	0	High	>500	0	Low	7.0	
S-8	625	0	High	500	0	Low	6.8	
S-10	1500		High	>500	0	Slight	7.8	5
S-12	575		High	>500	0	Low	6.0	3
S-13	325		High	>500		Low	7.0	3
S-15	1225		High	>500		Low	6.6	4
S-16	375		High	>500		Low	7.0	2
S-17	400		High	>500		Low	5.8	3
S-18	750		High	>500		Low	7.0	0

* ppm = parts per million.

SYSTEMATIC ANALYSIS

A check list of the animals found in this study is presented in Table 7. Wherever possible, the animals were determined by specialists in the taxonomy of the group concerned. In some cases determination is to genus or species, while in others it is to family or order. The number of animals actually collected and identified during the course of this work was 11,233. There were representatives of 5 phyla, 12 classes, and 37 orders in the collections.

One of the most striking features of work in the Neotropical rain forest is the great number of new species which one finds. This is especially true for the habitat under consideration, as few people bother to collect among the dead leaves of the surface litter when there is so much to be seen and collected in other niches. Those forms which have been determined as new, by experts in the taxonomy of the group concerned, are starred in the check list. There were 67 new species, 20 new genera, and one new family, and there are undoubtedly at least as many more new species in the material which has not yet been determined.

Tables 8 and 9 present the data for the animals collected on each quadrat. All of the quadrats are presented. In the case of the quadrats for which there was a Berlese analysis, the figures include those forms taken in the Berlese funnel, as outlined in the section under methods. The quadrats not used in the main analysis are starred.

Table 7. Check list of animals present in collections.†

Phylum Platyhelminthes
- Class Turbellaria
  - Order Alloeocoela
    - Family Prorhynchidae
      - *Geocentrophora tropica* Hyman*
  - Order Tricladida
  - Suborder Terricola
    - Family Geoplanidae
      - *Geoplana cameliae* Fuhrmann
      - *Geoplana panamensis* Hyman*
      - *Geoplana aphalla* Hyman*
    - Family Rhynchodemidae
      - *Desmorhynchus angustus* Hyman*
      - *Diporodemus plenus* Hyman*

Phylum Nemathelminthes
- Class Nematoda
  - Order Telogonia
  - Suborder Ascaroidea
    - Family Enoplidae
    - Subfamily Trilobinae
      - *Mononchus* sp.

† New species are indicated by (*), new genera by (**), and a new family by (***).

Subfamily Dorylaiminae
Dorylaimus sp.
Ironus sp.
Family Monhysteridae
Subfamily Monhysterinae
Monhystera sp.
Rotylenchus dihystera (Cobb, 1893)
Phylum Annelida
Class Oligochaeta
Class Hirudinea
Order Pharyngobdella
Family Herpobdellidae
Blanchardibdella decemoculata DeQual
Phylum Arthropoda
Class Crustacea
Order Isopoda
Family Oniscidae
Trichorhina isthmica Van Name
Trichoniscus (Clavigeroniscus) riquieri Arcangeli
Philoscia gatunensis Van Name
Philoscia (Ischioscia) variegata Dollfus
Scleropactes zeteki Van Name
Class Arachnida
Order Pedipalpida
Schizomus centralis Gertsch*
Order Scorpionida
Order Chelonethida
Order Phalangida
Family Phalangodidae 3 or 4 species
Family Gonyleptidae 1 species
Family Cosmetidae 1 or 2 species
Order Araneida
Family Dipluridae
Accola spinosa Petrunkevitch
Family Theraphosidae
Sericopelma rubronitens (Ausserer)
Family Ctenizidae
Idiops sp.
Ancylotrypa sp.
Family Ctenidae
Ctenus sp.
Cupiennius foliatus Cambridge
Family Heteropodidae
Tentabunda chickeringi Gertsch*
Olios sp.
Family Tetrablemmidae
Uniblemma unica Gertsch**
Family Zodariidae
Storena barroana Chamberlin
Family Argiopidae
Theridiosoma sp.
Mangora sp.
Eustala sp.
Aranea sp.
Pronous tuberculiferus Keyserling
Mimognatha foxi (McCook)
Family Linyphiidae
Bathyphantes plagiatus Banks

Family Theridiidae
Hubba insignis Cambridge
Stemmops sp.
Achaea acutiventer Keyserling
Euryopis sp.
Theridion indicatum Banks
Family Salticidae
Family Oonopidae
Oonopinus centralis Gertsch*
Scaphiella williamsi Gertsch*
Scaphiella barroana Gertsch*
Dysderina plena Cambridge
Family Caponiidae
Nops maculata Simon
Family Pholcidae
Metagonia caudata Cambridge
Modisimus dilutus Gertsch*
Pholcophorina zeteki Gertsch
Family Gnaphosidae
Lygromma chamberlini Gertsch*
Family Clubionidae
Myrmecotypus sp.
Castianeira sp.
Corinna sp.
Clubiona sp.
Family Anapidae
Anapis keyserlingi Gertsch*
Anapistula minorata Gertsch**
Anapisona reclusa Gertsch**
Order Acarina
Family Bdellidae
Eupalus sp.
Cunaxa sp.
Family Eupodidae
Genus ?
Eupodes sp.
Bimichaelia sp.
Rhagidia sp.
Tydeus sp.
Family Trombidiidae
Microtrombidium sp.
Immature specimens
Family Tetranychidae
Genus ?
Immature Specimens
Raphignathus sp.
Family Uropodidae
Genus ?
Family Parasitidae
Genus ?
Immature Specimens
Podocinum sp.
Family Labidostommatidae
Labidostomma sp.
Family Hoplodermatidae
Mesoplophora sp.
Phthiracarus sp.
Family Oribatidae
Genus ?

Immature Specimens
Belba (= *Oribata*) sp.
Carabodes sp.
Eremulus (= *Eremaeus*) sp.
Galumna sp.
Globozetes sp.
Hermannella sp.
Heterochthonius sp.
Hypochthonius sp.
Lohmannia sp.
Malaconothrus sp.
Nothrus sp.
Oppia sp.
Oribatella sp.
Oribotritia sp.
Pseudotritia sp.
Rostrozetes sp.
Scheloribates sp.
Sphaerobates sp.
Sphaerocthonius sp.
Xylobates sp.
Zetes sp.
Family Tyroglyphidae
Histioma sp.
Class Pauropoda
Order Heterognatha
Family Pauropodidae
Pauropus panamensis Hilton*
Class Diplopoda
Subclass Pselapognatha
Family Polyxenidae
Barroxenus panamanus Chamberlin**
Subclass Chilognatha
Order Limacomorpha
Family Glomeridesmidae
Glomeridesmus barricolens Chamberlin*
Glomeridesmus parvior Chamberlin*
Order Polydesmoidea
Suborder Polydesmidea
Family Stiodesmidae
Nabotomus delus Chamberlin**
Gasotomus dubius Chamberlin*
Dominicodesmus panamicus Chamberlin*
Family Stylodesmidae
Botryodesmus cryptus Chamberlin*
Family Oniscodesmidae
Oniscodesmus eutypus Chamberlin*
Barrodesmus isolatus Chamberlin**
Oncodesmus granosus (Gervais and Goudat)
Peltedo archimedes Chamberlin**
Family Eutynellidae***
Eutynellus flavior Chamberlin**
Suborder Strongylosomatidae
Family Leptodesmidae
Typophallus evidens Chamberlin**
Desmacrides dichrus Chamberlin**
Tichodesmus micrus Chamberlin**
Family Sphaeriodesmidae
Sphaeriodesmus isolatus Chamberlin*

Order Nematomorpha
Suborder Stemmiulidea
Family Stemmiulidae
Stemmiulus canalis Chamberlin*
Order Juliformia
Suborder Spirobolidea
Family Spirobolidae
Rhinocricus williamsi Chamberlin*
Microspirobolus sp.
Suborder Spirostreptomorpha
Family Spirostreptidae
Orthoporus sp.
Order Platydesmiformia
Family Polyzoniidae
Siphonotus centralis Chamberlin*
Siphonotus angulifer Chamberlin*
Family Siphonophoridae
Siphonophora fallens Chamberlin
Class Chilopoda
Subclass Epimorpha
Order Geophilomorpha
Family Schendylidae
Schendylurus (Schendylotyn) integer Chamberlin
Family Ballophilidae
Diplethemus dux Chamberlin*
Lepynophilus mundus Chamberlin**
Family Pachymerinidae
Polycricus fossor Chamberlin*
Family Chilenophilidae
Barrophilus isolatus Chamberlin**
Nabocodes mimellus Chamberlin**
Order Scolpendromorpha
Family Cryptopidae
Newportia rogersi Pocock
Subclass Anamorpha
Order Scutigeromorpha
Family Scutigeridae
Psellioides sp.
Class Symphyla
Order Cephalostigma
Family Scutigerellidae
Scutigerella panama Hilton*
Family Scolpendrellidae
Symphiella panama Hilton*
Class Hexapoda
Order Thysanura
Family Lepismatidae
Grassiella sp. (juvenile)
Family Campodeidae
Lepidocampa juradii Silv.
Campodea biolleyi Silv.
Campodea batesoni Silv.
Family Japygidae
Japyx tristani Silv.
Parajapyx isabellae (Grassi)
Order Collembola
Order Orthoptera
Family Blattidae
Blaberus sp.

Order Isoptera
- *Heterotermes tenuis* (Hagen)
- *Amitermes beaumonti* Banks
- *Microcerotermes arboreus* Emerson
- *Cylindrotermes macrognathus* Snyder
- *Anoplotermes* sp.
- *Nasutitermes (Uniformitermes) barrocoloradensis* Snyder
- *Nasutitermes (N.) ephratae* (Holmgren)

Order Neuroptera

Order Anoplura

Order Corrodentia
- Family Psocidae

Order Thysanoptera
- *Terthrothrips clavivestris* Hood

Order Homoptera

Suborder Auchenorrhyncha
- Super-family Cercopoidea
- Family Cercopidae nymphs
- Super-family Fulgoroidea nymphs
- Family Derbidae
  - *Mysidia* ? sp.
- Family Fulgoridae
- Subfamily Fulgorinidae nymphs
- Family Achilidae nymphs
- Family Flatidae
  - *Ormenis roscida* Germ. nymphs
  - *Flatormenis* sp. nymphs

Order Hemiptera
- Family Cydnidae
  - *Pangaeus* sp.
  - *Amnestus* sp.
- Family Aradidae
  - *Artagerus* sp.
- Family Lygaeidae
- Family Enicocephalidae
- Family Reduviidae
  - *Ectrichodia crudelis* Stal
  - *Rasahus* sp.
  - *Emesa* sp.
- Family Anthocoridae
- Family Miridae
- Family Cryptostemmatidae
  - *Nannocoris* sp.

Order Dermaptera
- Family Labiduridae
  - *Psalis* sp.
  - *Euborellia annulipes* (Lucas)

Order Trichoptera
- Family Hydroptilidae

Order Diptera
- Family Psychodidae
  - *Psychoda* sp.
- Family Ceratopogonidae
  - *Culicoides diabolicus* Hoff.
- Family Culicidae
  - *Anopheles* sp.
- Family Cecidomyidae
- Family Stratiomyidae (larvae)
- Family Tabanidae
  - *Dichelocera analis* Hine

Family Dolicopodidae
Paracleius obscurus V. D.
Family Phoridae
Puliciphora sp.
Chonocephalus sp.
Megaselia sp.
Family Drosophilidae
Drosophila sp.
Family Chloropidae
Oscinella sp.
Family Borboridae
Leptocera sp.
Order Coleoptera
Family Carabidae
Apenes five species
Masoreus sp.
Notobia umbrifera Bts.
Notobia sp.
Abaris darlingtoni Str.
Loxandrus two species
Loxandrus tetrastigma Bts.
Tachys two species
Genus ? near *Agonum*
Family Hydrophilidae
Phaenonotum sp.
Oosternum sp.
Genus ? near *Dactylosternum*
Family Silphidae
Aglyptinus sp.
Family Scaphidiidae
Scaphidium sp.
Genus ?
Family Scydmaenidae
Family Staphylinidae
Subfamily Oxytelinae
Subfamily Omaliinae
Subfamily Paederinae
Tribe Pinophilini
Tribe Paederini
Subfamily Staphylininae
Tribe Xantholinini
Tribe Staphylinini
Subfamily Tachyporinae
Tribe Tachyporini
Erchomus sp.
Subfamily Aleocharinae
Family Pselaphidae
Tribe Jubinini
Jubus terranus Park*
Jubus chickeringi Park*
Jubus turneri Park*
Barrojuba albertae Park**
Tribe Euplectini (*sensu latiore*)
Eurhexius zonalis Park*
Panaramecia williamsi Park**
Tribe Batrisini
Arthmius (*Arthmius*) *sabomba* Park*
Tribe Tyrini
Juxtahamotopsis bardeni Park**

Family Lampyridae
- *Silis* sp.
- *Silis* sp. near *oblita* Gohr.

Family Dryopidae
- *Parnus pusillus* Sharp

Family Elateridae (larvae)

Family Dermestidae (larvae)

Family Dascylidae
- *Ptilodactyla* sp.

Family Histeridae
- *Bacanius hamatus* Lewis
- *Epierus schmidti* Wenzel and Dybas*
- *Hister foveipygus* Wenzel and Dybas*
- *Phelister williamsi* Wenzel and Dybas*
- *Phelisteroides panamensis* Wenzel and Dybas*

Family Nitidulidae
- *Stelidota strigosa* (Gyll.)

Family Endomychidae
- *Micropsephodes* sp.
- Genus ?

Family Coccinellidae
- *Hyperaspis* sp.

Family Ptiliidae

Family Tenebrionidae
- *Anaedus*, five species
- Genus ? three species

Family Cerambycidae (larva)

Family Curculionidae
- *Phyllotrox* sp.
- *Anchonus* sp.
- *Eubulus* sp.
- *Conotrachelus* sp.
- *Palaeopus* sp. apparently new

Subfamily Cossoninae
- New genus and species

Family Ipidae
- *Pityophthorus* sp. near *incompositus* Bldfd.
- *Xyleborus propinquus* Eichh.
- *Xyleborus affinis* Eichh.
- *Coccotrypes* sp.
- *Stephanoderes* sp.

Family Scarabaeidae
- *Canthon angustatus* Har.
- *Canthon moniliatus* Bates
- *Canthon sallei* Har.
- *Uroxys* sp. near *micros* Bates
- *Choeridium aeneomicans* Har.
- *Canthidium* sp.
- *Phyllophaga* sp.
- *Ataenius*, three species

Order Lepidoptera (larvae)

Family Geometridae (larvae)

Order Hymenoptera

Family Eulophidae
- *Melittobia* sp.
- *Tetrasticus hagenowi* (Ratz.)

Family Calliceratidae
- *Calliceras* sp.
- Genus ?

Family Formicidae
Subfamily Dorylinae
Eciton (Labidus) coecum Latr.
Subfamily Ponerinae
Ectatomma ruidum Rog.
Alfaria panamensis Weber*
Discothyrea isthmica Weber*
Pachycondyla harpax (Fabr.)
Pachycondyla striata F. Smith
Termitopone laevigata (F. Smith)
Ponera sp.
Ponera sp. near *trigona*
Ponera parva Forel
Leptogenys (Lobopelta) n. sp. probably
Odontomachus chelifer Latr.
Odontomachus haematoda L.
Anochaetus sp. (not *mayri, inermis meinerti,* or *bispinosus*)
Neoponera apicalis Latr.
Subfamily Pseudomyrminae
Pseudomyrma sp.
Subfamily Myrmicinae
Pheidole sp. probably including one or two n. sp.
Solenopsis sp.
Megalomyrmex (Cepobroticus) wheeleri Weber
Megalomyrmex (Cepobroticus) symmetochus Wheeler
Crematogaster sp.
Aphaenogaster (Deromyrma) sp. near *phalangium* Emery
Wasmannia sp.
Leptothorax n. sp.
Rhopalothrix sp. near *equilatera* Weber
New dacetonine genus
Strumigenys brevicornis Mann
Strumigenys n. sp. near *S. emeryi* Mann and *fusca* Emery
Strumigenys n. sp.
Strumigenys eggersi Emery
Strumigenys tristani Menozzi
Cyphomyrmex rimosus Spinola
Cyphomyrmex costatus Mann
Sericomyrmex amabalis Wheeler
Trachymyrmex isthmicus Santschi
Trachymyrmex cornetyi Forel sp. *gatun* Weber
Trachymyrmex morgani Weber
Apterostigma mayri Forel
Cephalotes atratus (L.)
Subfamily Dolichoderinae
Azteca sp.
Subfamily Formicinae
Nylanderia steinheili (Forel)
Nylanderia sp.
Brachymyrmex n. sp.
Rhizomyrma n. sp.
Camponotus (Dinomyrmex) agra (F. Smith)
Camponotus (Myrmobrachys) sp.
Camponotus sp.

Phylum Mollusca
Class Gastropoda

Table 8. Small Quadrats—Record of Collections

	1	*2*	*3**	*4**	*5*	*6**	*7*	*8*	*9**	*10*	*11**	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*Total for Quadrats with Berlese*
Turbellaria	1		1		1					2	3		2						6
Nematoda	1	20		1	7	3	28	1		8		3	2	17		6		1	94
Oligochaeta	10	27	8	6	15	7	18	11	15	24	2	5	10	42	2	9	5	4	182
Hirudinea	1		1		3			1			1		2	3					10
Isopoda	34	33		3	32	15	4	5	9	21	9	6	18	6	9	8	8	4	188
Pedipalpida	3														2				5
Chelonethida	3	6	6	1	7	4	1	4	4	12	3	25	24	4	1	12		6	105
Phalangida	4	2	2	2				1	3	1	2				2	1		6	17
Araneida	6	6	5	4	1	1	3	2	5	8	3	8	9	3	1	2	1	3	53
Acarina	101	248	79	30	90	9	105	144	24	116	8	194	288	149	211	96	106	201	2049
Pauropoda		7	1	1	2			16	1	4		5	3			4	2		43
Diplopoda	20	13	13	4	20	9	5	24	11	12	6	13	17	10	9	10	3	18	174
Chilopoda		1		1						2			3	1	1		3	1	12
Symphyla	3				1				4			1	3	3		8	2		21
Thysanura	3	9	5	3	3	4		20	2	3	1	5	1	6	2	3	1	3	59
Collembola	102	228	7	8	51	5	30	124	10	180	8	219	624	270	154	236	127	239	2584
Orthoptera	1	5	1	2	1	2	1	4	2	2	2		1	1	3	1		4	24
Isoptera								4	10			7		3					14
Neuroptera larvae			1																
Anoplura		2								1									3
Thysanoptera						1													
Homoptera		1					2	4		4			2	4		4		1	22
Hemiptera	4	2	1		2	2	1	3	2	1	1		9	3	1		1	1	28
Dermaptera												1							1
Coleoptera larvae	14	7	11	1	10	2	1	4	6	6	2	3	12	8	5	3		4	77
Coleoptera adults	37	10	1	2	13	3	6	20	9	36		4	13	5	5	3	5	5	162
Lepidoptera larvae	1	1					2				1	2	2					1	9
Diptera larvae	4	10	4	1		8	5	5		9		1	7	3	1	4		1	50
Diptera adults		1	1		9	1	2			6	4			1	3	3		5	30
Hymenoptera larvae												1	1		1				3
Hymenoptera adults										1									1
Formicidae	67	290	170	2	185	10	133	28	55	526	22	168	156	77	14	160	3	11	1818
Insect larvae							1	1					1						3
Gastropoda	15	3	3	3	8	9	2	21	21	43	11	6	7	13	2	3	4	11	138
Total	435	932	321	75	461	95	350	447	193	1028	89	677	1217	632	429	576	271	530	7985

**No Berlese Analysis*

Table 9. Large Quadrats—Record of Collections

	*1**	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Totals for Quadrats with Berlese*
Turbellaria	3	1	1	1		2	1	4		5		15
Nematoda		3		3	3		2			12	6	29
Oligochaeta	14	72	30	20	7	32	85	12	12	40	49	359
Hirudinea				1					3	3	1	8
Isopoda	25	17	68	46	44	64	70	47	122	123	42	643
Pedipalpida										1	1	2
Scorpionida						1						1
Chelonethida			15	47		28	17	35	30	32	4	208
Phalangida	8	10	11	24	57	33	5	9	8	27	2	186
Araneida	10	16	17	15	22	24	3	18	18	12	19	164
Acarina	20	29	124	450	424	677	578	1575	1440	1792	2142	9231
Pauropoda			22		23		18	34	120	32	119	368
Diplopoda	49	24	28	69	40	22	34	67	21	70	81	456
Chilopoda		1	2	16	3	27	4	1	2	3	8	67
Symphyla				15	22	3	3		1	31	7	82
Thysanura	2		7	77	67	28	33	2	60	8	120	402
Collembola	1	22	51	527	1204	902	770	1015	1950	4736	2975	14152
Orthoptera	2	3	9	10	3	6	8	8	12	7	12	78
Isoptera		1	11		1			1	6	22		42
Corrodentia						1			1			2
Anoplura				6								6
Thysanoptera larvae					3							3
Homoptera	1		1	2		1	1				7	12
Hemiptera	1	1	5	2	27	9	6	30	8	28	4	120
Dermaptera			3									3
Coleoptera larvae	5	11	6	7	3	10	9	14	7	48	8	123
Coleoptera adults	8	5	10	16	29	26	55	44	13	89	49	336
Lepidoptera larvae			3	1					1	7	1	13
Diptera larvae	7	13	9	5	3	4		4	6	41	42	127
Diptera adults	2		1	15	2	1	17	5	2	2	1	46
Hymenoptera pupae	2		1									1
Hymenoptera adults				10		1	10			2		23
Formicidae	129	88	117	388	245	367	108	49	600	384	8211	10557
Insect pupae					1							1
Insect larvae									1	9		10
Gastropoda	5	11	19	6	23	15	16	6	6	42	12	156
Total	294	328	571	1779	2256	2284	1853	2980	4450	7608	13923	38032

**No Berlese Analysis*

In the following section the various taxonomic groups are considered separately as regards their occurrence—indicated by the percentage of total number of quadrats on which representatives were found, and in regard to density—indicated by the percentage of the total population which the particular group represents. Other factors pertaining specifically to the individual groups are also considered.

Phylum Platyhelminthes

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	38	.08
Large quadrats	70	.04

The most common species was *Desmorhynchus angustus* Hyman, being present on 17 per cent of the small quadrats and 36 per cent of the large ones. In all there were six species present in the collections. Two orders and three families were represented.

The fact that only 38 per cent of the small quadrats contained planaria, while 70 per cent of the large ones did, is indicative of the relative scarcity of these forms. They must be considered as an important component of the litter fauna, but they apparently require a comparatively large area for subsistence.

Dr. L. H. Hyman who identified the planaria stated that most of the forms were not sexually mature. This may be an indication that the breeding takes place earlier in the year, perhaps at the start of the rainy season. On the other hand, it may mean that many of the adults do not carry over from year to year, and these forms were produced the previous year and would have matured and mated toward the end of the rainy season.

Phylum Nemathelminthes

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	85	.08
Large quadrats	60	1.18

Nematodes were found on a significant number of quadrats, but the number collected is probably not a true picture of their abundance. Collection by Berlese funnel is not satifactory for these forms and, because of their small size, a large proportion were probably missed in the manual

collections. It is also possible that the nematodes are more a part of the true soil fauna and their presence in the surface litter may be purely adventitious. Further work, in which adequate methods of collecting nematodes are employed, will be necessary before one can say just how important they are in the litter stratum.

The most commonly occurring as well as the most abundant group were *Dorylaimus* sp., as they were found on 85 per cent of the small quadrats and 60 per cent of the large. Four other genera were represented in the collections.

Phylum Annelida

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	2.40
Large quadrats	100	.95

Two classes of the phylum were present, the Oligochaeta and the Hirudinea. The former are more properly considered as soil forms and their presence in the litter is more or less by chance, as is suggested also for the Nemathelminthes. The Hirudinea may be considered as residents of the surface stratum.

Class Oligochaeta

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	2.27
Large quadrats	100	.93

I was unable to find anyone to determine the earthworms, so it is not possible to indicate any characteristic group.

Class Hirudinea

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	46	.13
Large quadrats	40	.02

The leeches were all of a single species, *Blanchardibdella decemoculata* De Qual. Dr. J. P. Moore, who identified them, stated that the gut of those sectioned contained the remains of small insect larvae. If this is indicative of the food of all these forms it would seem that the leech is

definitely a part of the floor stratum. The insect larvae are abundant there and, for a terrestrial form which requires a high humidity, the floor stratum would be the most favorable niche in the forest.

The species was described from Costa Rica and this is a new record of its occurrence. Dr. Moore found that although the specimens were sexually mature, they were considerably smaller than those from Costa Rica.

Phylum Arthropoda

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	94.61
Large quadrats	100	98.53

In the tropical rain forest the phylum Arthropoda reaches a peak of diversification and is by far the most characteristic and abundant phylum of the litter stratum. Seven of its classes and thirty-one of its orders were present in the collections. The representatives of this phylum so far out-number all other groups that one might consider the others insignificant.

The onychophoran, *Peripatus*, did not appear in any of the collections. This form, confined to the tropics, has been reported from Barro Colorado Island but in the last few years none have been collected. Some people claim that the ardor of collectors decreased the population to the vanishing point, but it is probable that *Peripatus* is still to be found on the island, even though it is not abundant.

Class Crustacea

Order Isopoda

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	2.35
Large quadrats	100	1.67

The order Isopoda was the only order of Crustacea represented in the collections. The most characteristic species was *Philoscia (Ischioscia) variegata* Dollfus, which was found on 100 per cent of the large and small quadrats. Another species of the same genus, *Philoscia gatunensis* Van Name, was found on 72 per cent of the small quadrats and 64 per cent of the large ones. It is interesting to note that four of the five species reported by Van Name (1926) were found, and one additional species was present. Van Name states that these species are entirely

native, forest-living species, that there are no introduced forms, and that this absence of introduced forms, "confirms the existence of purely natural ecological conditions."

The isopods were very much in evidence in all of the collections. An interesting behavior of some species was their ability to jump considerable distances, in much the same exasperating manner that is characteristic of collembola. Because of this habit, collection of all the forms present in the large quadrats was practically impossible, and to some extent this accounts for the difference in the population densities for the large and small quadrats.

Class Arachnida

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	27.85
Large quadrats	100	25.13

The Arachnida, mainly because of the great number of Acarina, are a very important component of the floor fauna. Six orders of this class were present in the collections.

Order Pedipalpida

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	15	.06
Large quadrats	20	.005

One species of the order Pedipalpida was found, *Schizomus centralis* Gertsch.

Order Scorpionida

One scorpion was found on one of the large quadrats.

Order Chelonethida

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	92	1.31
Large quadrats	80	.54

The pseudoscorpions are very small organisms which may be said to be characteristic of the litter, inasmuch as they occur in such a large proportion of the quadrats.

Order Phalangida

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	61	.21
Large quadrats	100	.48

Three families of harvestmen were present: Phalangodidae, Gonyleptidae, and Cosmetidae. The Phalangodidae were the most abundant, being found on 61 per cent of the small quadrats and 100 per cent of the large.

Order Araneida

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	.66
Large quadrats	100	.10

Spiders were found in all of the quadrats, but as they are carnivorous in their feeding habits, it is not surprising that they form a small percentage of the total population. This does not lessen their importance as a major member of the community.

Seventeen families of the order Araneida were represented. The data on the occurrence of these families is given in Table 10. There is

Table 10. Occurrence of Families of Araneida

Family	*Percentage of Total Quadrats*	
	Small	Large
Dipluridae	8	0
Theraphosidae	15	50
Ctenizidae	15	10
Ctenidae	31	90
Heteropodidae	0	40
Tetrablemmidae	0	10
Zodariidae	30	50
Argiopidae	0	60
Linyphiidae	8	50
Theridiidae	0	40
Salticidae	8	30
Oonopidae	76	80
Caponiidae	15	10
Pholcidae	8	70
Gnaphosidae	0	30
Clubionidae	8	40
Anapidae	15	10

a considerable discrepancy between the values obtained for the large and small quadrats. This difference is in part due to the fact that the spiders tend to move about considerably and during the course of the four or five hours collecting of the material on the large quadrat there would be a movement of some of these forms into the area being studied. The family Oonopidae, in which the values for the large and small quadrats are comparable (76 and 80 per cent), was represented by rather minute species and in this case the movement would be confined to a relatively small range. Another, more important, reason is that the spiders are carnivorous and therefore tend to be less numerous than herbivorous forms. The smaller size of the 25 cm. quadrat would not be as likely to include spiders so the percentage of small quadrats including spiders would tend to be low. Many of the species were found only on the large quadrats, and then only one or two specimens were collected.

The most common species was *Oonopis centralis* Gertsch, found on 76 per cent of the small quadrats and 80 per cent of the large ones. Another common one was *Cupiennius foliatus* Cambridge, found on 30 per cent of the small and 90 per cent of the large quadrats.

Order Acarina

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	25.61
Large quadrats	100	24.00

The Acarina are one of the three dominant groups of arthropods present in the litter. They are a very important component of the fauna, forming an appreciable part of the base of the food chain. The results for both large and small quadrats are comparable in both percentage of the total population and percentage of the quadrats on which Acarina occurred.

The late Dr. A. P. Jacot had very kindly agreed to make the determinations of the Acarina. Due to his unfortunate death data are available for only twelve of the small quadrats. All of the information here will be based on these quadrats.

Ten families of mites were represented. The occurrence of the families, given as the percentage of the total number of quadrats on which they were found, is presented in Table 11.

Table 11. Occurrence of Families of Acarina

Families	*Percentage of Total Number of Quadrats*
Bdellidae	58
Eupodidae	74
Trombidiidae	25
Tetranychidae	58
Uropodidae	100
Parasitidae	100
Labidostommatidae	33
Hoplodermatidae	33
Oribatidae	100
Tyroglyphidae	33

The three families occurring on 100 per cent of the twelve quadrats, and a fourth on 74 per cent, Uropodidae, Parasitidae, Oribatidae, and Eupodidae respectively, may be considered as the characteristic families. The oribatids were the most numerous. The genera *Scheloribates* and *Sphaerobates* are the most characteristic of the family Oribatidae, being found on 80 per cent and 42 per cent of the quadrats respectively. Of the Eupodidae, the genus *Eupodes* occurred on 75 per cent of the quadrats, *Bimichaelia* on 58 per cent and *Tydeus* on 50 per cent. The genus *Podocinum* (Parasitidae) occurred on 58 per cent of the quadrats.

Class Pauropoda

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	61	.54
Large quadrats	70	.96

These small, colorless arthropods were represented by one species, *Pauropus panamensis* Hilton.

Class Diplopoda

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	2.18
Large quadrats	100	1.19

The millipeds are another very characteristic group, being found on all quadrats. They may also be considered important because they form a comparatively large percentage of the population. Six orders and thirteen families of Diplopoda were present. The data for these families are presented in Table 12.

Table 12. Occurrence of Families of Diplopoda

Family	*Percentage of Total Number of Quadrats*	
	Small	Large
Polyxenidae	38	50
Glomeridesmidae	23	50
Stiodesmidae	23	10
Stylodesmidae	7	0
Oniscodesmidae	76	50
Eutynellidae	46	60
Leptodesmidae	69	70
Sphaeriodesmidae	23	20
Stemmiulidae	53	50
Spirobolidae	23	30
Spirostreptidae	8	0
Polyzoniidae	0	10
Siphonophoridae	30	20

There is a rather close correlation between the small and large quadrats in this group, as opposed to the condition found in the Araneida. The millipeds are herbivorous and would not be limited as a carnivorous form might be. The families Leptodesmidae and Oniscodesmidae were represented by the greatest number of species and were found on the greatest percentage of the quadrats. The occurrence of the four most characteristic species is given in Table 13.

Table 13. Most Abundant Diplopod Species

Species	*Percentage of Total Number of Quadrats*	
	Small	Large
Barroxenus panamanus Chamberlin	38	50
Barrodesmus isolatus Chamberlin	38	40
Eutynellus flavior Chamberlin	46	60
Stemmiulus canalis Chamberlin	53	50

Class Chilopoda

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	54	.15
Large quadrats	100	.17

The centipedes are a carnivorous group and their distribution on the forest floor is similar to that described for the spiders. They form a small percentage of the total population and they did not occur on all of the small quadrats. There were 3 orders and 6 families present. The data for the families are presented in Table 14.

Table 14. Occurrence of Families of Chilopoda

Family	*Percentage of Total Number of Quadrats*	
	Small	Large
Cryptopidae	15	50
Scutigeridae	10	0
Schendylidae	8	0
Ballophilidae	0	40
Pachymerinidae	8	10
Chilenophilidae	31	40

No particular family stands out as a characteristic one. The most common species were not particularly widespread, as indicated in Table 15.

Table 15. Most Abundant Chilopod Species

Species	*Percentage of Total Number of Quadrats*	
	Small	Large
Barrophilus isolatus Chamberlin	31	30
Diplethemus dux Chamberlin	0	40
Newportia rogersi Pocock	15	50

Class Symphyla

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	61	.26
Large quadrats	70	.21

Two families of this class, represented by one species each, were found in the collections. It is interesting that in only one case were both species found on the same quadrat.

Class Hexapoda

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	61.11
Large quadrats	100	67.75

The class Hexapoda, due to the large numbers of Collembola and Formicidae, is the most important class of animals in the litter fauna; sixteen orders and fifty-four families were identified. The number of families would be higher if identification to at least this level had been possible in all groups.

Order Thysanura

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	92	.74
Large quadrats	90	1.05

Although the bristletails comprise a relatively small percentage of the total population, they can be considered as characteristic animals because they occur on such a large percentage of the quadrats. The most common species was *Japyx tristani* Silv., occurring on 67 per cent of the small quadrats and 45 per cent of the large. Almost as common, was *Lepidocampa iuradii* Silv., on 55 per cent and 45 per cent of the small and large quadrats respectively.

Order Collembola

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	32.30
Large quadrats	100	36.80

The Collembola are the most abundant group of animals in the litter fauna. They are the most characteristic animals of the litter, if abundance and occurrence are taken as criteria of characteristic animals. They form the main base of the food chain and, as such, are very important in the general picture of the floor fauna.

Order Orthoptera

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	92	.30
Large quadrats	100	.20

The Orthoptera present on the quadrats were all nymphs except in the case of one adult roach (*Blaberus* sp.). These nymphs were almost all of the family Blattidae. The scarcity of adults would seem to indicate that breeding occurred either at the end of the rainy season and the nymphs collected were the offspring of the previous year's breeding, or that the breeding occurred just at the start of the rainy season.

Order Isoptera

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	31	.18
Large quadrats	60	.11

The scarcity of the termites in the forest floor litter was indeed a surprise. This group is very widespread in the tropics and forms a very important part of the fauna. In spite of the fact that each twig was carefully broken open and all woody material carefully examined, the number of termites found was very low. Further work on this particular problem is necessary before a satisfactory answer can be given. Allee (1926) in speaking of the fauna of rotten logs present on the forest floor at Barro Colorado Island says, "the large number of termites (present in rotten logs) emphasizes the fact that these insects are much more likely to be found in decaying wood than ranging free on the forest floor."

Of the seven species present, the most abundant was *Heterotermes tenuis* (Hagen). This species was found on 23 per cent of the small quadrats and 10 per cent of the large ones.

Order Neuroptera

One Neuroptera larva was found on one of the small quadrats.

Order Anoplura

Anoplura were found on 15 per cent of the small and 10 per cent of the large quadrats. These forms made up a very insignificant part of the total population (.04 and .03 per cent respectively).

Order Corrodentia

One member of the family Psocidae was found on each of two large quadrats. These forms were .005 per cent of the total population.

Order Thysanoptera

One adult thrip, *Terthropthrips clavivestris* Hood, was found on a small quadrat and three larvae were found on one large quadrat.

Order Homoptera

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	69	.27
Large quadrats	60	.03

There were five families of this order represented. Most of the specimens were nymphs. The most characteristic family was the Flattidae, being found on 33 per cent of the small quadrats and 20 per cent of the large ones.

Order Hemiptera

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	92	.35
Large quadrats	100	.31

The true bugs were well represented as far as occurrence on the two types of quadrats is concerned. There were eight families represented. A great many of the specimens were nymphs. The most characteristic family was the Lygaeidae with 69 per cent of the small and 70 per cent of the large quadrats having this group present. Two other groups, Cryptostemmatidae and Reduviidae, were well represented on the large quadrats, but not on the small. The former was present on 38 per cent of the small and 80 per cent of the large quadrats, while the latter was found on 23 per cent of the small quadrats and 70 per cent of the large ones.

Order Dermaptera

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	8	.01
Large quadrats	10	.005

Two species of earwigs were found, a single specimen of *Psalis* sp. on one small quadrat and three specimens of *Euborellia annulipes* (Lucas) on a large quadrat.

Order Trichoptera

One specimen of the family Hydroptilidae was found on a small quadrat.

Order Diptera (adults)

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	61	.37
Large quadrats	100	.12

Diptera adults formed a small portion of the total population, but they occurred on a significantly large percentage of the quadrats. Ten families were represented. The only family present on any appreciable number of quadrats was the family Psychodidae, represented by the genus *Psychoda* on 30 per cent of both the large and small quadrats.

Order Diptera (larvae)

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	92	.63
Large quadrats	100	.33

The Diptera larvae form a more important part of the litter fauna than do the adults. The larvae of only one family were identified, the family Stratiomyidae, and these forms were found on 53 per cent of the small and 60 per cent of the large quadrats.

Order Coleoptera (adults)

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	2.03
Large quadrats	100	.87

The Coleoptera are a characteristic group of animals of the litter. There were twenty-two families of this order present. Inasmuch as several of these families are rather important members of the litter fauna they will be considered separately.

Family Carabidae

The ground beetles were found on 23 per cent of the small and 70 per cent of the large quadrats. These carnivorous forms are wide ranging and relatively fast moving, and it is probable that the high percentage for the large quadrats is in part due to their wandering into the quadrat during the course of the collection. It is also true that these carnivorous forms must have a relatively large range and the chance of their occurring on the one-sixteenth of a square meter quadrat is not as great as that of their occurring on a meter quadrat. This same discrepancy is reflected in the occurrence of particular species; *e. g.*, *Notobia umbrifera* Bts. was found on 40 per cent of the large quadrats and not on any of the small ones. In like manner, *Loxandrus* "species 1 and 2" were each found on 30 per cent of the large quadrats and not on any small ones.

Family Hydrophilidae

Hydrophilids were found on 38 per cent of the small quadrats and 30 per cent of the large ones. A genus near *Dactylosternum* was found on 31 per cent of the small quadrats but not on any large ones.

Families Silphidae, Scaphidiidae, and Scydmaenidae

Family	OCCURRENCE *Percentage of Total Number of Quadrats*	
	Small	Large
Silphidae	8	0
Scaphidiidae	15	0
Scydmaenidae	53	30

The Scydmaenidae are the only group to warrant special mention.

Family Staphylinidae

Staphylinids were present on 77 per cent of the small quadrats and 100 per cent of the large ones. They may be said to be characteristic Coleoptera of the litter fauna. Six sub-families were present. The Tachyporinae, genus *Erchomus,* were found on 80 per cent of the large and 23 per cent of the small quadrats. The Aleocharinae were present on 90 per cent of the large quadrats and 46 per cent of the small ones.

Families Pselaphidae, Lampyridae, Dryopidae, and Dascylidae

Family	OCCURRENCE *Percentage of Total Number of Quadrats*	
	Small	Large
Pselaphidae	46	80
Lampyridae	0	8
Dryopidae	8	10
Dascylidae	0	10

The Pselaphidae were present on a large enough percentage of the quadrats to be considered as characteristic forms. Professor Park has kindly given me permission to use information which will appear in his forthcoming monograph of the Neotropical Pselaphidae. For the genus *Batrisodes,* closely related to some genera which occur on Barro Colorado Island, he states:

> The food averages considerably less than a millimeter in length and appears to be the minute floor larvae and mold mites (Parasitidae, Gamasidae, Hoplodermatidae) of the forest floor. Consequently they compete with such small forms as *Atheta* (Staphylinidae) and many Scydmaenidae (*Enconnus cavipennis* Casey, *Connophron, Eumicrus*). Previous observations (Park, 1932) indicate that some pselaphids are scavengers as well, feeding on dead animals; and other data (Park, 1935) indicate that they may be cannibalistic, and also attack much larger game than mold mites, for example, earthworms.

For another species, *Tmesiphorus costalis* LeConte, which has allies in the Panama rain forest, Park states *(loc. cit.)*

. . . . *costalis* is a carnivore. It has been seen feeding upon the larvae of *Aphaenogaster fulva*, as well as the eggs and pupae of the host. In its more usual habitat away from the ant nests, the species has been seen to attack and eat mold mites (Hoplodermatidae) and minute flies *(Sciara)*.

Family Histeridae

There were five species of histerids in the collections. They occurred on 15 per cent of the small quadrats and 70 per cent of the large ones. *Phelister williamsi* Wenzel and Dybas was collected on 8 per cent of the small quadrats and 70 per cent of the large ones. We find here another group with many predacious members that shows a definite tendency to have a comparatively large range, therefore not occurring on as many of the small quadrats.

Families Nitidulidae, Endomychidae, and Coccinellidae

Family	OCCURRENCE *Percentage of Total Number of Quadrats*	
	Small	Large
Nitidulidae	0	20
Endomychidae	8	10
Coccinellidae	0	10

It is probable that these occurrences are purely adventitious and these families would not be considered as characteristic of the litter fauna.

Family Ptiliidae

These minute Coleoptera were found on 85 per cent of the small and 60 per cent of the large quadrats. One may consider them to be rather characteristic of the floor fauna.

Family Tenebrionidae

The tenebrionids were represented in 23 per cent of the small quadrats and 80 per cent of the large ones. The most characteristic forms were two species of an undetermined genus occurring on 40 per cent of the large quadrats and 8 per cent of the small ones. As the family was found on 80 per cent of the large quadrats, it is a characteristic family of the litter fauna.

Family Curculionidae

Weevils were found on 15 per cent of the small quadrats and 40 per cent of the large. This occurrence is not high enough to consider the family as characteristic. No particular group within the family was found on a significant percentage of the quadrats.

Family Ipidae

The Ipidae, another group of small beetles, were collected on 39 per cent of the small quadrats and 30 per cent of the large ones. These forms cannot be considered as characteristic of the floor fauna. The commonest representative of the family was *Xyleborus propinquus* Eichh., occurring on 31 per cent of the small and 20 per cent of the large quadrats.

Family Scarabaeidae

The scarabs were found on 15 per cent and 60 per cent of the small and large quadrats respectively. Although the figures are not very high, it seems that the family should be considered a characteristic one. These are comparatively large beetles, and it is likely that their small showing is due to the fact that all of the larger forms occur less abundantly than the smaller ones.

Summary of Coleoptera Adults

Table 16 gives those families of the order Coleoptera which, by reason of their occurrence on at least 60 per cent of the large quadrats, may be considered as characteristic of the litter fauna.

Table 16. Characteristic Families of Coleoptera

Family	OCCURRENCE *Percentage of Total Number of Quadrats* Small	Large
Carabidae	23	70
Staphylinidae	77	100
Pselaphidae	40	80
Histeridae	15	70
Ptiliidae	85	60
Tenebrionidae	23	80
Scarabaeidae	15	60

The most characteristic family of the order is the family Staphylinidae. The discrepancies between the occurrence on the large and small quadrats indicate that the large quadrats give a more adequate picture of the larger forms present. The smallest beetles, family Ptiliidae, were found on a greater number of small quadrats than large. This may be a result of the fact that the large quadrats were collected in the field and these very small forms might have been overlooked in some cases.

Order Coleoptera (larvae)

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	.96
Large quadrats	100	.32

The Coleoptera larvae are a significant part of the litter fauna. Determination to family was not possible in all cases, but Table 17 presents the data where identification was possible.

Table 17. Occurrence of Coleoptera Larvae

Family	*Percentage of Total Number of Quadrats*	
	Small	Large
Family undetermined	100	90
Carabidae	23	80
Hydrophilidae	8	10
Staphylinidae	62	50
Lampyridae	8	40
Tenebrionidae	0	30
Scarabaeidae	15	20
Elateridae	54	30
Dermestidae	15	0
Cerambycidae	0	20

The Carabidae, Staphylinidae, and perhaps the Elateridae might be considered as the most characteristic beetle larvae present.

Order Coleoptera (larvae and adults)

A consideration of the occurrence of some of the more characteristic families, in which the larvae and adults are placed together, accentuates the fact that they are really characteristic of the litter fauna. Three families are affected by such a treatment and the data are given in Table 18.

Table 18. Characteristic Coleoptera (larvae and adults)

Family	OCCURRENCE *Percentage of Total Number of Quadrats*	
	Small	Large
Carabidae	38	100
Staphylinidae	85	100
Scarabaeidae	31	60

Order Lepidoptera (larvae)

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	46	.11
Large quadrats	50	.03

The Lepidoptera, represented in the surface litter by larvae only, are not a particularly characteristic order. The family Geometridae was the only group determined, and it was found on 15 per cent of the small quadrats and 20 per cent of the large.

Order Hymenoptera

	OCCURRENCE *Percentage of Total Number of Quadrats*	DENSITY *Percentage of Total Population*
Small quadrats	100	22.78
Large quadrats	100	27.50

The order Hymenoptera is one of the three dominant groups present in the litter fauna. This dominance is due entirely to the ants, family Formicidae, as the other groups present are insignificant. In addition to the Formicidae, two other families were present, the Eulophidae and Calliceratidae.

Family Formicidae

Six subfamilies of ants were present, and each will be considered separately. The ants, a wide ranging and highly carnivorous group of animals, are of great importance in the food relationships of the forest floor. They prey upon all of the other arthropods of the stratum and in turn they are also a source of food for a great many animals. The stomach contents of *Bufo marinus* (L.), the giant toad which occurs on Barro Colorado Island, were studied by Weber (1938) in Trinidad and British Guiana. He found that a large part of the food of this toad was made up of ants. Many of the same species reported here were found in the toad stomachs. Albert Barden found that a lizard, *Basiliscus basiliscus* (L.), had 26.7 per cent ants in its food.

It is interesting that the percentage of occurrence of the various subfamilies in this study agrees with the abundance of these same subfamilies reported by Weber in the stomach analysis of *Bufo marinus* (L.). Such analyses may be rather important additions to the other quantitative methods, for those groups of animals which are likely to be eaten by the forms studied.

The Myrmicinae and Ponerinae may be considered as the characteristic subfamilies of ants. These two groups were found on the greatest percentage of quadrats and were represented by the greatest number of species, Myrmicinae being ahead of the Ponerinae in both respects.

Subfamily Dorylinae

Eciton (Labidus) coecum Latr., one of the army ants, was the only representative of this subfamily. It was found on only one small quadrat. This is not surprising, as the army ant colonies move about from place to place and would be abundant locally, but rather scarce over the entire area.

Subfamily Ponerinae

This group is the second most widespread subfamily of ants in the collections, occurring on 54 per cent of the small and 100 per cent of the large quadrats. The three most characteristic species, as shown by their high percentage of occurrence, especially in the large quadrats, are *Pachycondyla harpax* (Fabr.) and *Odontomachus haematoda* L., found on 70 per cent of the large and 8 per cent of the small quadrats, and *Anochaetus* sp., found on 60 per cent of the large and 15 per cent of the small quadrats. The other species were found on only one or two quadrats each.

Subfamily Pseudomyrminae

One representative of this subfamily, *Pseudomyrma* sp., was on one small quadrat.

Subfamily Myrmicinae

The Myrmicinae, found on 100 per cent of both the small and large quadrats, are the most common group of ants. The genus *Solenopsis* was the most characteristic as members of this genus were present on 92 per cent of the small and 90 per cent of the large quadrats. *Pheidole* was the next important genus, found on 69 per cent and 100 per cent of the small and large quadrats respectively. *Cyphomyrmex rimosus* Spinola occurred on 31 per cent of the small quadrats and 60 per cent of the large ones.

Subfamily Dolichoderinae

One large quadrat contained representatives of *Azteca* sp.

Subfamily Formicinae

This group was found on 15 per cent of the small and 40 per cent of the large quadrats. It would not be classed as a characteristic group on this basis. The species were scattered in distribution, no single one occurring on more than 10 or 15 per cent of the quadrats.

Phylum Mollusca

The Mollusca, all of the class Gastropoda, may be considered as characteristic forms of the floor fauna, as they occurred on all of the quadrats. The population densities were 1.04 per cent and .40 per cent for the small and large quadrats respectively.

DISCUSSION OF RESULTS

SUMMARY OF FAUNAL ANALYSIS

In the preceding section, each group has been considered in some detail and it seems advisable to point out some aspects of the fauna as a whole.

Faunal Percentages

The population density, as indicated by the percentage of the total population which a particular group represents, is given for the main taxonomic divisions in Table 19 for the small and large quadrats.

Table 19. Faunal Percentages.

Group	*Percentage of Total Population*	
	Small Quadrats	Large Quadrats
Turbellaria	.08	.04
Nematoda	1.18	.08
Oligochaeta	2.27	.93
Hirudinea	.13	.02
Isopoda	2.35	1.67
Pedipalpida	.06	.005
Scorpionida		.003
Chelonethida	1.31	.54
Phalangida	.21	.48
Araneida	.66	.10
Acarina	25.61	24.00
Pauropoda	.54	.96
Diplopoda	2.18	1.19
Chilopoda	.15	.17
Symphyla	.26	.21
Thysanura	.74	1.05
Collembola	32.30	36.60
Orthoptera	.30	.20
Isoptera	.18	.11
Corrodentia		.005
Anoplura	.04	.02
Thysanoptera		.008
Homoptera	.27	.03
Hemiptera	.35	.31
Dermaptera	.01	.008
Coleoptera larvae	.96	.32
Coleoptera adults	2.03	.87
Lepidoptera larvae	.11	.03
Diptera larvae	.63	.33
Diptera adults	.37	.12
Hymenoptera	.05	.06
Formicidae	22.73	27.44
Gastropoda	1.73	.40

Because a great portion of the population is made up of three groups of animals, the Collembola, Acarina, and Formicidae, the relationships in the other groups are somewhat obscured. In order to show these relationships more clearly, the three groups mentioned have been treated as single units and all of the other animals have been lumped in a fourth. The data are presented in Table 20. The fourth group was then treated as a separate unit and the population percentages calculated, after the Acarina, Collembola, and Formicidae had been removed. These data are found in Table 21.

Table 20. Faunal Percentages

Group	*Percentage of Total Population*	
	Small Quadrats	Large Quadrats
Acarina	25.61	24.00
Collembola	32.30	36.80
Formicidae	22.73	27.44
All others	19.36	11.76

Table 21. Faunal Percentages
(Excluding Acarina, Collembola, and Formicidae)

Group	*Percentage of Total Population*	
	Small Quadrats	Large Quadrats
Turbellaria	.39	.37
Nematoda	5.81	.71
Oligochaeta	11.83	8.76
Hirudinea	.65	.20
Isopoda	12.22	15.69
Pedipalpida	.33	.05
Scorpionida		.02
Chelonethida	6.83	5.08
Phalangida	1.11	4.54
Araneida	3.45	4.00
Pauropoda	2.80	8.98
Diplopoda	11.31	11.13
Chilopoda	.78	1.63
Symphyla	1.37	2.00
Thysanura	3.84	9.81
Orthoptera	1.56	1.90
Isoptera	.91	1.00
Corrodentia		.05
Anoplura	.20	.15
Thysanoptera		.07
Homoptera	1.43	.29
Hemiptera	1.82	2.93
Dermaptera	.07	.07
Coleoptera larvae	5.00	3.00
Coleoptera adults	10.53	8.20
Lepidoptera larvae	.59	.32
Diptera larvae	3.25	3.01
Diptera adults	1.95	1.12
Hymenoptera	.26	.59
Gastropoda	8.97	3.81

Occurrence

The percentage of the quadrats containing representatives of a given group is another index of a characteristic group. It is not necessary for a group to be present in great numbers before it is considered characteristic. If only a few examples are found on each quadrat, it can be considered more than chance. One would therefore expect to find the order represented in any sample one might take. Table 22 contains the data for the occurrence of the main taxonomic groups.

Table 22. Occurrence of Main Taxonomic Groups

Group	*Percentage of Total Number of Quadrats*	
	Small	Large
Turbellaria	38	70
Nematoda	85	60
Oligochaeta	100	100
Hirudinea	46	40
Isopoda	100	100
Pedipalpida	15	20
Scorpionida		10
Chelonethida	92	80
Phalangida	61	100
Araneida	100	100
Acarina	100	100
Pauropoda	61	70
Diplopoda	100	100
Chilopoda	54	100
Symphyla	61	70
Thysanura	92	90
Collembola	100	100
Orthoptera	92	100
Isoptera	31	60
Corrodentia		20
Anoplura	15	10
Thysanoptera	8	10
Homoptera	69	60
Hemiptera	92	100
Dermaptera	8	10
Coleoptera larvae	100	100
Coleoptera adults	100	100
Lepidoptera larvae	46	50
Diptera larvae	92	100
Diptera adults	61	100
Hymenoptera	15	40
Formicidae	100	100
Gastropoda	100	100

Raunkiaer Analysis

Raunkiaer (1918), a European worker, devised an interesting method of analysis which gives the index species of a community or any portion of a community. The number of quadrats upon which a given species is found is the frequency index and the percentage of occurrence is the frequency percentage. The frequency percentages are thrown into five

classes: I, 1 to 20 per cent; II, 21 to 40 per cent; III, 41 to 60 per cent; IV, 61 to 80 per cent; and V, 81 to 100 per cent. When these data are graphed, one obtains a typical curve, which is usually found in similar studies of any natural population. The data for both the small and large quadrats were treated in this manner and may be found in Table 23 and the graphs in Figures 1 and 2.

Table 23. Raunkiaer Analysis
Distribution of the Frequency Percentages

Group	Class I		Class II		Class III		Class IV		Class V	
	S	*L*	*S*	*L*	*S*	*L*	*S*	*L*	*S*	*L*
Turbellaria	3	1	2	3	0	0	0	0	0	0
Nematoda	4	1	0	1	0	0	0	1	1	0
Hirudinea	0	0	0	0	1	1	0	0	0	0
Isopoda	1	1	0	2	1	0	0	2	2	1
Araneida	14	20	2	12	0	6	1	1	0	1
Pauropoda	0	0	1	0	0	0	0	1	0	0
Diplopoda	4	3	9	7	2	5	1	1	0	0
Chilopoda	3	4	1	1	0	2	0	0	0	0
Symphyla	0	0	2	1	0	1	0	0	0	0
Isoptera	2	4	1	1	0	0	0	0	0	0
Coleoptera	23	32	4	10	0	3	0	1	0	1
Formicidae	22	17	4	9	0	3	1	4	1	2
Totals	76	83	26	47	4	21	3	11	4	5

S - Small Quadrats
L - Large Quadrats

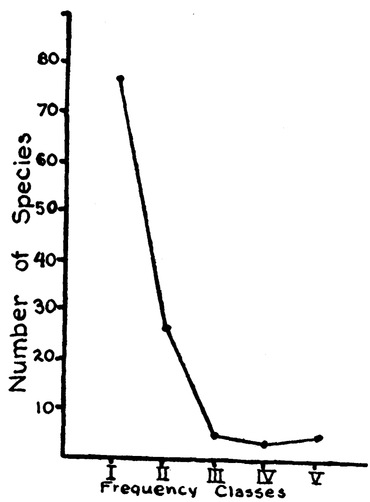

Fig. 1. Raunkiaer analysis - small quadrats

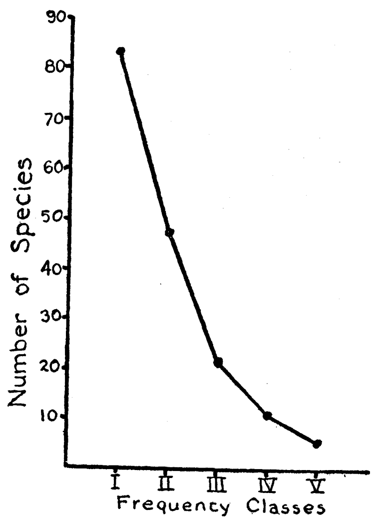

Fig. 2. Raukiaer analysis - large quadrats

The index species, those that fall in Class V, are: ***Dorylaimus*** sp. (Nematoda), *Philoscia gatunensis* Van Name and ***Philoscia variegata*** Dollfus (Isopoda), *Cupiennius foliatus* Cambridge (Araneida), ***Erchomus*** sp. (Staphylinidae), *Pheidole* sp. and *Solenopsis* sp. (Formicidae).

The graphs show an interesting character of any natural population. Most of the species are found at random and rather infrequently over a given area. Only a very small percentage of the species occurs in considerable numbers and in any part of the region studied. The so-called index species, those that are found throughout the area, seem to be the best adapted to their particular habitat. The index species may be slightly better adjusted to one particular phase of the environment and this slight advantage over the other closely related forms enables them to occupy a large portion of the territory. The fact that there are only seven index species, representing five orders, indicates that the remaining species are probably about equally balanced in their adjustments and competition between species limits the number which can inhabit the area.

Characteristic Groups

It is not possible to designate a truly dominant group of forest litter animals, in accordance with the definition of dominance given by Shelford and Clements (1939). In this more or less sheltered habitat none of the animals may be said to receive the full impact of the environment. In fact, it would be difficult to pick out any animal in the tropical rain forest and call it a dominant. The plants, mainly the large trees, are the only true dominant living forms. It appears that we are justified, however, in speaking of certain groups of animals as characteristic of the litter fauna.

It has been pointed out that certain forms are found on a large percentage of the large quadrats and on a smaller percentage of the small ones. The suggestion was made that the carnivores and larger herbivores, requiring a relatively large range, would not necessarily be collected on any one small quadrat, but would appear on a significant portion of the large ones.

On the basis either of large population density and/or occurrence on at least 70 per cent of the large or small quadrats, those groups considered to be characteristic of the litter fauna are presented in Table 24.

Number of Species

It has already been mentioned that in the tropics in general the number of species present is large and the number of individuals of each species is correspondingly lowered. In spite of the fact that determination in many cases could not be obtained, there were 294 different

Table 24. Characteristic Groups of the Litter Fauna

Group	*Percentage Occurrence*		*Percentage of Total Population*	
	Small	Large	Small	Large
Turbellaria	33	70	.08	.04
Nematoda	85	60	1.18	.08
Oligochaeta	100	100	2.27	.93
Isopoda	100	100	2.35	1.67
Chelonethida	92	80	1.31	.54
Phalangida	61	100	.21	.48
Araneida	100	100	.66	.10
Acarina	100	100	25.61	24.00
Pauropoda	61	70	.54	.96
Diplopoda	100	100	2.18	1.19
Chilopoda	54	100	.15	.17
Symphyla	61	70	.26	.21
Thysanura	92	90	.74	1.05
Collembola	100	100	32.30	36.80
Orthoptera	92	100	.30	.20
Hemiptera	92	100	.35	.31
Diptera adults	61	100	.37	.12
Diptera larvae	92	100	.63	.33
Coleoptera adults	100	100	2.03	.87
Coleoptera larvae	100	100	.96	.32
Formicidae	100	100	22.73	27.44
Gastropoda	100	100	1.73	.40

species, determined either to species or to genus. In contrast, Dr. Elizabeth Lunn in a study of the fauna of the leaf mold in a forest near Evanston, Illinois (1939) found 111 different species. The difference is all the more striking because practically all of her material was determined to species. In the case of this material, there are at least 100 more species which can be added to the total when all of the determinations are available.

This large number of species in the tropics may be in part due to the great abundance of food of various kinds and the wide variety of habitat niches. Evolutionary tendencies which lead a particular group to become associated with a particular habitat niche or food would have a definite survival value, especially if it were a food or habitat for which there was little competition. The great variety of these two factors, food and habitat, may possibly be an important item in the development of the great variety of species present.

QUANTITATIVE ASPECTS OF THE PROBLEM

The number of animals present in the litter of the Panama rain forest floor is perhaps best illustrated by Figure 3. This figure shows the average number of animals of each group found on one-tenth of a square meter. The animals have been drawn to scale, the size for each group being the average size of all those collected. The animals in their natural

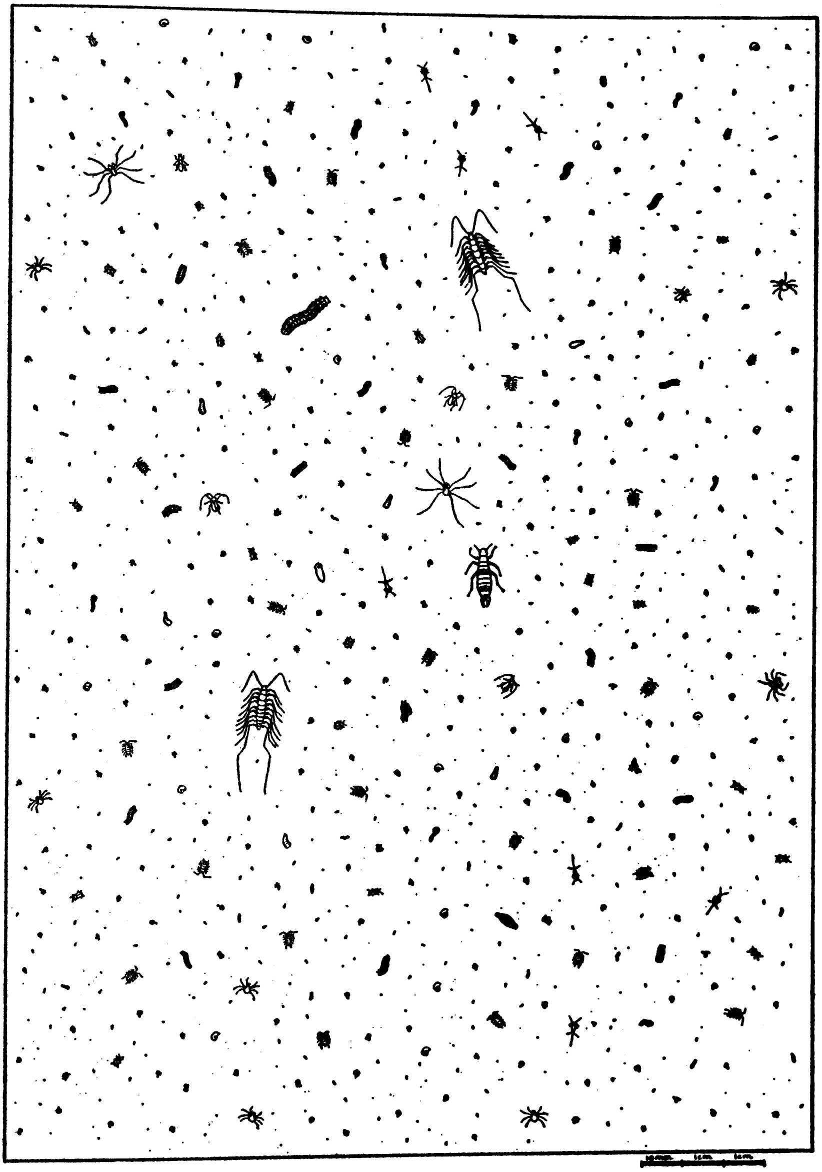

Fig. 3. Diagram of average population on one-tenth of a square meter, based on small quadrats.

habitat are of course not on a single plane, but are distributed throughout the leaf mold which may be from two to five inches thick. The very small circles indicate the Acarina, and the Collembola are represented by small circles with a line drawn out to indicate the furcula. Other forms are stylized and are large enough to be recognized.

Number per Square Meter

Based on the small quadrats, there was an average of 9,822 animals per square meter. This amounts to approximately 40,000,000 per acre. The average for the large quadrats is somewhat lower, 3,803 per square meter, or about 15,500,000 per acre. The highest value for any one small quadrat was 19,472 per square meter (79,000,000 per acre) and the highest value for a large quadrat was 13,923 per square meter (56, 000,000 per acre).

Biomass

Lunn (1939) determined the biomass (Pickles, 1937) by weighing the more common animals found in her study of the leaf and log mold of Carlé Woods, Des Plaines, Illinois. She found that there were 33.35 pounds of microarthropods and oligochaetes per acre of forest floor (leaf mold). Facilities were not available for making accurate measurements of the weights for the animals in this study, so the figures given by Dr. Lunn in her work are used. These figures are given in Table 25.

Table 25. Approximate Average Weight in Grams of Forest Floor Animals (From Lunn, 1939)

	Grams
Oligochaeta	.002
Coleoptera larvae	.02
Coleoptera adults	.03
Diptera larvae	.002
Trachelipus rathkei (an Isopod)	.03
Collembola	.000025
Acarina	.000025

On the basis of these figures there were 15.53 grams present on each square meter, or 138 pounds per acre. This figure is merely an approximation and it is based on the assumption that on the average the weights for the particular groups are comparable. The true figure would be considerably higher, as the great number of ants and all of the other minor groups were not included. In fact, these results based on the small quadrats include only 6,509 of the 9,822 animals on a square meter (67 per cent). The mass of available food material is shown to be very appreciable and a more comprehensive study of this problem of the biomass is desirable.

Eltonian Pyramid

In dealing with the number of animals present in a given community, the fact that the greatest number of animals is found in the smallest size range is very evident. Charles Elton (1936) has been a leading student of animal populations. He devised a method of expressing this relationship of numbers and size, the so-called Eltonian Pyramid. The number of animals present is plotted against their size. The data for the small quadrats have been treated in this manner and the resulting pyramid may be found in Figure 4. The data upon which this figure is based are in Table 26. The sizes used are the average sizes for all of the members of the group found in the collections.

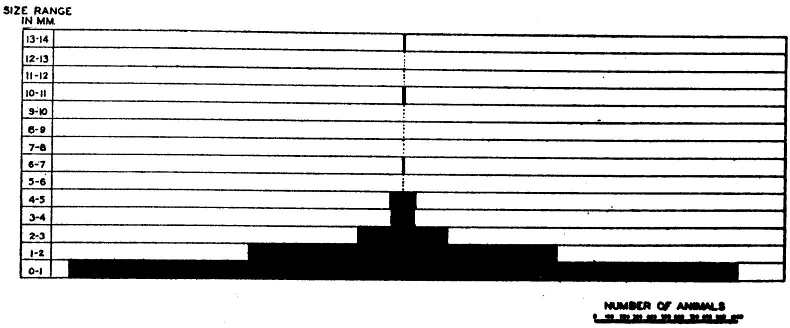

Fig 4. Eltonian pyramid of numbers, based on small quadrats.

The bearing of this problem on the food relations of the forest floor is fairly obvious. The basis of the food for all animals is the plant matrix. We find the minute Collembola and Acarina forming the broad base of the pyramid, and in general these forms are herbivorous. As we move toward the apex of the pyramid, we find the carnivorous forms present in smaller numbers. In general, one may say that the carnivorous animals are larger and are present in smaller numbers than the herbivorous forms upon which they feed. Carnivores also feed upon other carnivores and upon scavengers, and the prey is usually smaller than the predator. This latter condition, however, does not hold true for the ants. The Formicidae, falling in the 1 to 2 mm. size range, are present in large numbers and they are carnivorous for the most part. Because of their closely integrated social organization, a great many ants may attack a much larger animal and, while the size of any single ant is insignificant, in the aggregate their "size" is tremendous. Under certain conditions, organisms thousands of times the size of an individual ant may be the victim of the ants collectively.

Table 26. Data for Eltonian Pyramid (small quadrats)

Size range	*No. on 13 small quadrats*
0 - 1 mm.	
Acarina	2049
Nematoda	94
Pauropoda	43
Collembola	2584
1 - 2 mm.	
Chelonethida	105
Anoplura	3
Homoptera	22
Diptera adults	30
Formicidae	1818
Insect larvae	3
Araneida	53
Symphyla	21
Hymenoptera	4
Gastropoda	138
2 - 3 mm.	
Oligochaeta	182
Pedipalpida	5
Phalangida	17
Hemiptera	28
Coleoptera adults	162
Isopoda	188
Thysanura	59
3 - 4 mm.	
Coleoptera larvae	77
Diptera larvae	50
Orthoptera	24
Isoptera	14
4 - 5 mm.	
Diplopoda	174
Turbellaria	6
6 - 7 mm.	
Hirudinea	10
10 - 11 mm.	
Chilopoda	12
13 - 14 mm.	
Dermaptera	1
Lepidoptera larvae	9

Very little is known about the food habits of organisms living in the forest floor litter. When it comes to those of the tropical rain forest litter, nothing is known specifically. Although some broad generalizations can be made in regard to possible food relations, further study is necessary before any definite statement about the food chain is possible.

RELATION OF THE FAUNA TO ENVIRONMENTAL FACTORS

Physical Factors

Soil Analysis. The data for the soil analysis have been presented in Table 6. Of the factors determined, the only ones which varied significantly were the hydrogen ion concentration (pH) and potassium (K).

The number of animals present does not seem to be correlated with the K content of the soil. Figures 5 and 6 show the number of animals

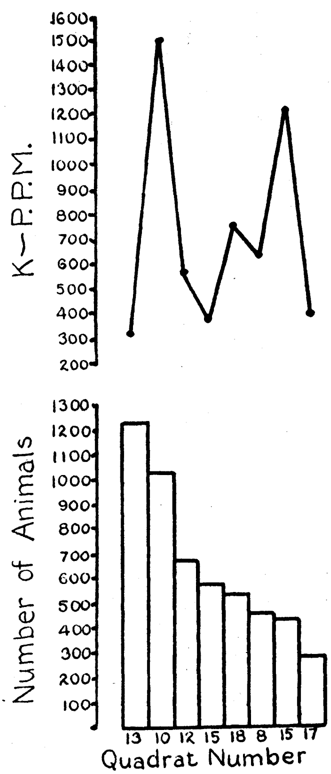

Fig. 5. Relationship between the number of animals present and the potassium content of the soil - small quadrats.

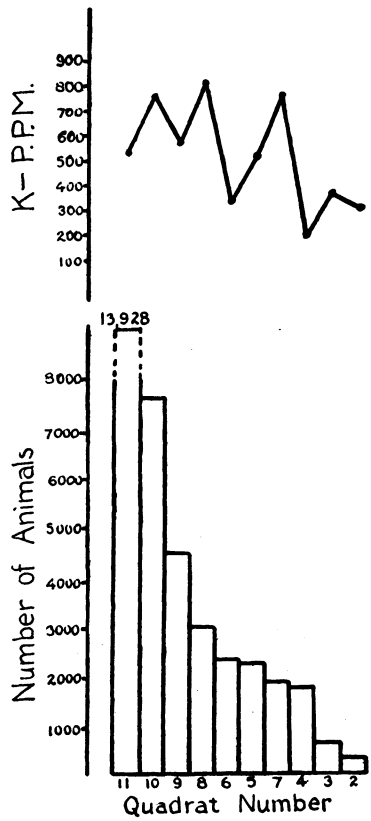

Fig. 6. Relationship between the number of animals present and the potassium content of the soil - large quadrats.

present in the lower portion and the variation in K is plotted above. In the case of the small quadrats the lowest value for K was found on the quadrat containing the most animals, while the highest value was found on the quadrat with the second greatest number of animals. In the large quadrats, likewise, there is no apparrent correlation between the K content of the soil and the number of animals present.

The pH in relation to the number of animals present is graphically shown in Figures 7 and 8. There is a mere suggestion, especially in the small quadrats, that high population values are associated with a neutral condition, but it is no more than a suggestion.

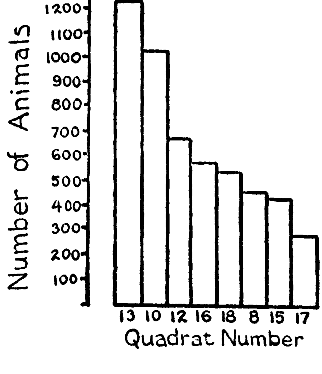

Fig. 7. Relationship between the number of animals present and the hydrogen ion concentration of the soil - small quadrats.

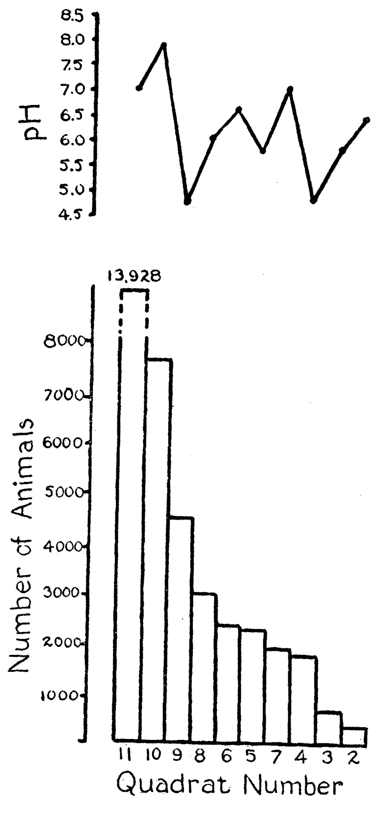

Fig. 8 Relationship between the number of animals present and the hydrogen ion concentration of the soil - large quadrats.

Soil Moisture. The soil moisture values, presented in Table 5, have been plotted above the histograms for population density in Figures 9 and 10. There seems to be some correlation between the number of animals present and the soil moisture. The soil moisture is indicative of the conditions in the leaf mold. It is probable that the minute forms, with with their thin body walls, require a very high moisture. Lunn (1939) found that Acarina moved to the chamber with the highest humidity

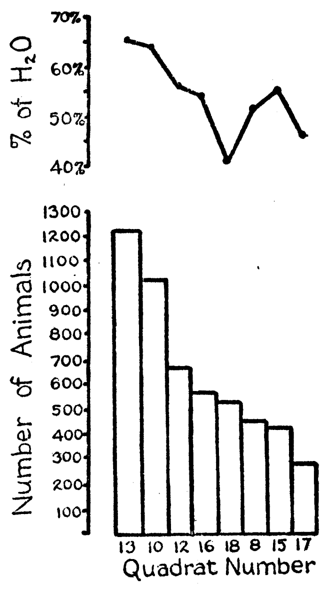

Fig. 9. Relationship between the number of animals present and the water content of the soil - small quadrats.

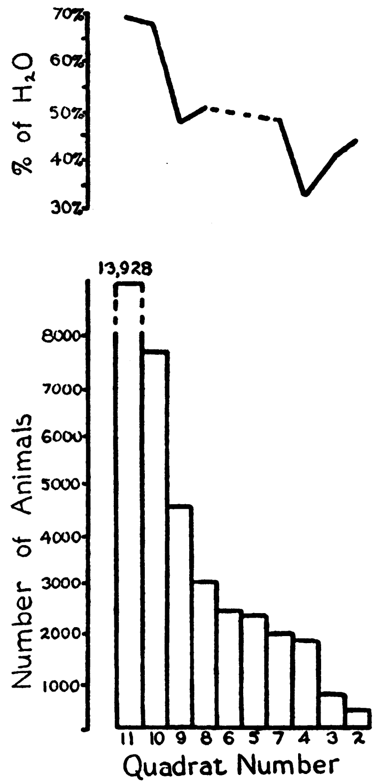

Fig. 10. Relationship between the number of animals present and the water content of the soil - large quadrats.

when placed in a gradient. Ford (1938) found that Collembola moved to the base of grass clumps when it was dry and under more humid conditions they were found on the grass itself. In those quadrats with low moisture values, these minute forms may move into the soil, as the moisture there would be higher than in the leaf mold.

Rainfall. In view of the apparent tendency for the population density to be related to the moisture, it seemed advisable to determine whether or not there was any fluctuation in population correlated with rainfall. (The rainfall record for the period of study is given in Table 1). There was no apparent direct correlation between the number of animals present and the rainfall. A comparison of the population densities with the amount of rainfall in the six hours preceding collection gave negative results, (Figure 11). A similar comparison for 1, 2, 3, 4, and 5 hours

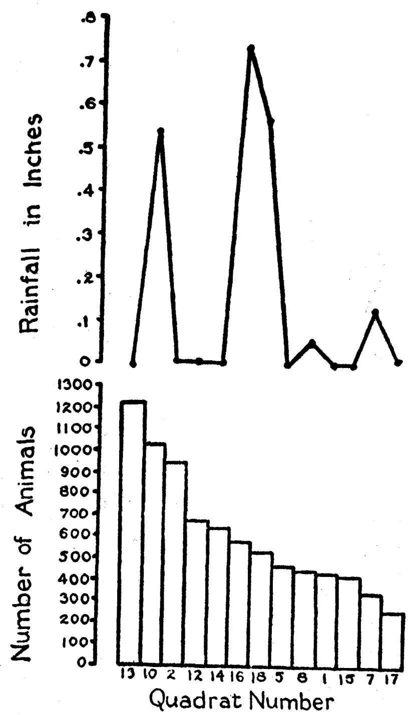

Fig. 11. Relationship between the number of animals present and the amount of rainfall in the six hours preceding time of collection - small quadrats.

preceding collection also gave negative results. The forest canopy offers such a large surface that the amount of rain falling to the floor is considerably less than that falling in the open where the rainfall measurements were made. The force of its fall is also broken and in many cases the drops are broken up to give more of a mist on the forest floor itself.

Biotic Factors

Amount of Leaf Mold. One would expect that the number of animals present would vary to some extent with the amount of leaf mold. The amount of leaf mold (in grams) has been plotted above the histograms for population density in Figures 12 and 13. The small quadrats show this trend very well, especially when it is noted that there were several large pieces of bark on quadrat 15, and not very much leaf mold. The trend is also evident in the large quadrats, but is not as well defined. It cannot be said that the amount of leaf mold, above a certain minimum, is a direct factor in controlling the abundance of organisms, but it is a

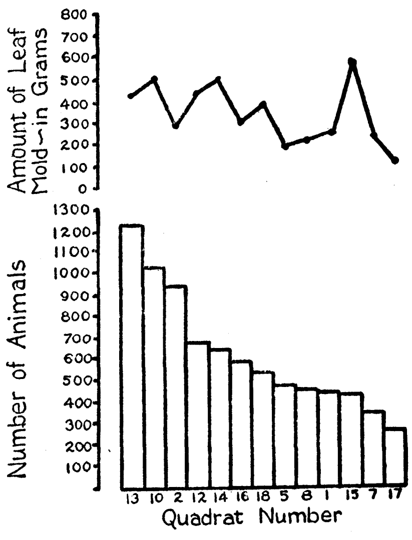

Fig. 12. Relationship between the number of animals present and the amount of leaf mold - small quadrats.

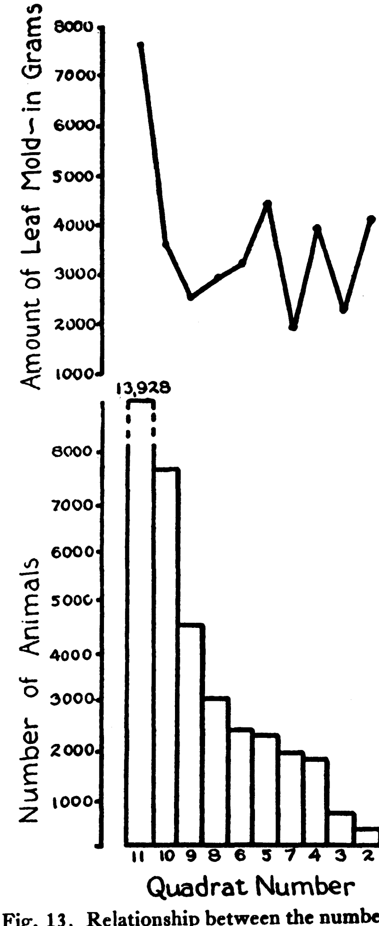

Fig. 13. Relationship between the number of animals present and the amount of leaf mold - large quadrats.

factor which has at least an indirect effect. Within certain limits it is probably not an important factor, but very little mold and large quantities of it must be considered as factors in control of the number of organisms.

Army Ants. The army ants constitute the only predator factor which could be correlated with population densities. The raiding columns of these ants pass through a given area and capture or drive out a large portion of the animal life. In two cases there was definite evidence that army ants had raided the area the day before collection. In both cases the population density was at a minimum, and it may be that low values in other instances are due to the same cause.

Population Fluctuations

Diurnal. The large quadrats were all collected in the daytime, and collection usually took from 9 A.M. to 3 or 4 P.M. The small quadrats were taken at various times during the day. A study of the population densities did not show any fluctuation that could be correlated with the time of collection.

Nocturnal. Two quadrats, S-4 and S-6, were collected at night. They were taken at 11 P.M. and 10 P.M. respectively. It was not possible to obtain a Berlese analysis for these two quadrats; they were kept over-night in an aluminum can and sorted out the following morning. The values for these two quadrats are low—75 and 95 animals. The average value for the other small quadrats, exclusive of those forms taken in the Berlese analysis, is 209. With only two quadrats taken at night, one cannot draw any conclusions, but they both gave low values and further study may show some difference in the number of forms present at night. There are two possible explanations for the condition, either the animals retreat into the soil, or they move up into the trees and shrubs (Park, Lockett, and Myers, 1931, and Park and Strohecker, 1936).

Seasonal. In Figure 14 the number of animals collected is plotted against the date of collection. The gradual increase in number of forms found on the large quadrats may be due to two causes. To some extent there was an improvement in collection technique for the first few quadrats, but this does not appear to be the only reason for the gradual rise. The results for the large quadrat on July 19 and the first small quadrat on July 20 are strictly comparable and they indicate that the methods may be comparable throughout. A suggestion regarding this fluctuation may be in order. During the dry season, from January through April, the rainfall is very low and a large number of forms probably do not survive. This season of the year may be compared to the winter of temperate zones. With the onset of the rainy season in

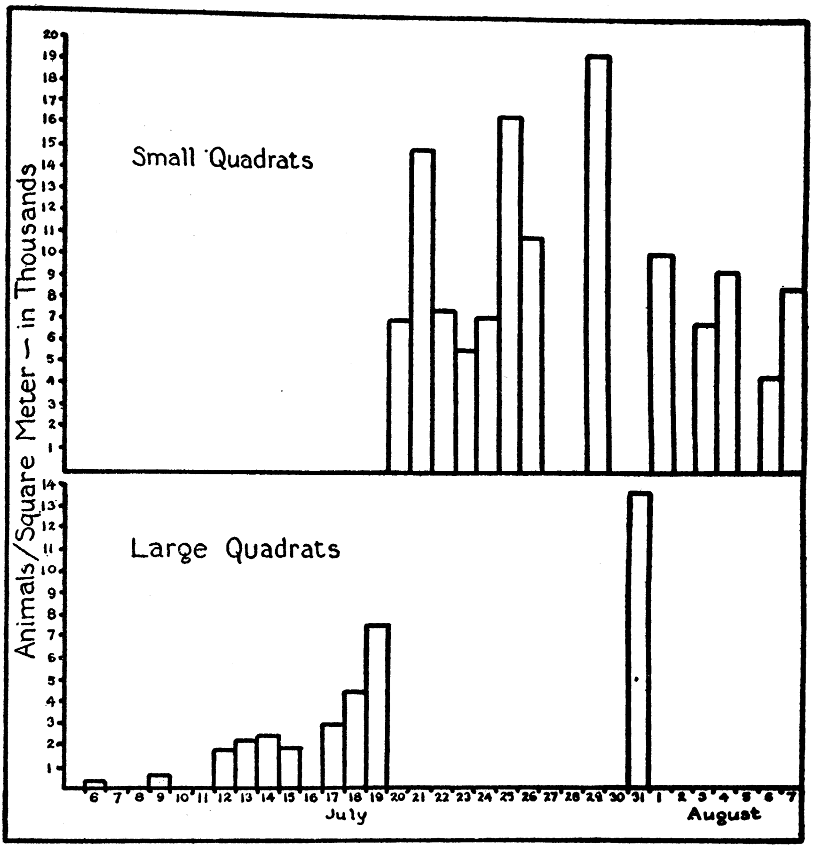

Fig. 14. Relationship between the number of animals present and the date of collection - small and large quadrats.

May, life in the litter begins with renewed vigor and those forms which have survived the dry season commence to reproduce. There would be a certain amount of lag in the population growth and not until the early part of July would the population begin to rise appreciably. This is the time when the collections reported here were commenced. It has been shown above that there was some correlation between the soil moisture and the population density. The earlier large quadrats show considerably lower moisture values than the later ones. Dammerman (1925, 1937) found that the low point in population of the litter fauna in the East Indies was reached in the dry season, and a peak occurred in the wet season. A more thorough study will be necessary, with collections made in the dry season, before one can say that there is a seasonal fluctuation and that the results obtained here are really a reflection of this fluctuation.

ACKNOWLEDGMENTS

I am deeply indebted to Professor Orlando Park for invaluable suggestions in the field, for the determination of the Pselaphidae, and for his constant guidance and inspiration during the entire course of this research. I would like to acknowledge the kindness of Mr. James Zetek, custodian of Barro Colorado Island, who did many things to facilitate my work in the Panama Canal Zone.

It is impossible for one to be sufficiently familiar with all groups of animals to make accurate taxonomic determinations. In a problem such as this, one must call upon specialists in the various groups. I am very grateful to the following persons for their kindness in making the determinations:

L. H. Hyman, Platyhelminthes
J. R. Christie, Nematoda
J. P. Moore, Hirudinea
W. G. Van Name, Isopoda
W. J. Gertsch, Arachnida (except Acarina)
A. P. Jacot, Acarina
W. A. Hilton, Pauropoda, and Symphyla
R. V. Chamberlin, Chilopoda and Diplopoda
F. Silvestri, Thysanura
Alfred Emerson, Isoptera
J. D. Hood, Thysanoptera
Z. P. Metcalf, Homoptera
W. J. Gerhard, Hemiptera (Heteroptera)
A. B. Gurney, Orthoptera, Dermaptera and Trichoptera
C. H. Curran, Diptera
T. J. Daggy, Diptera larvae and Coleoptera larvae
P. J. Darlington, Carabidae
H. B. Leech, Hydrophilidae
C. H. Seevers, Staphylinidae
Orlando Park, Pselaphidae
R. L. Wenzel, Histeridae
W. S. Fisher, Silphidae and Endomychidae
H. S. Barber, Scaphidiidae, Lampyridae, Dascylidae, and Dryopidae
E. A. Chapin, Tenebrionidae, Scarabaeidae, Nitidulidae, and Coccinellidae
L. L. Buchanan, Curculionidae and Hydrophilidae
M. W. Blackman, Ipidae
C. F. W. Muesebeck, Hymenoptera
N. A. Weber, Formicidae

SUMMARY

Methods of collection used in this study are described. Two sizes of quadrat were used, eleven of them were one meter square and eighteen of them were twenty-five centimeters square.

The general habitat and the floor stratum are described.

An analysis of the environmental factors, especially rainfall, relative humidity, temperature, and soil is presented.

A check list of the animals found includes representatives of five phyla, twelve classes, and thirty-seven orders.

A systematic analysis of the various taxonomic groups is included.

Faunal percentages were computed for each order. The Acarina, Collembola, and Hymenoptera (Formicidae) make up 80.64 per cent of the animals on the small quadrats and 88.24 per cent of those on the large.

The percentage of occurrence for each order represented was calculated and the characteristic groups, based on occurrence on at least 70 per cent of the large or small quadrats or a large population density, are indicated.

Analysis of the population by the method of Raunkiaer resulted in typical curves for both the large and small quadrats, indicating that most of the species are not very numerous, only seven of them occurring on 80 per cent or more of the quadrats.

The large number of species is characteristic of tropical faunas; 289 species have been determined to date. There were 67 new species, 20 new genera, and one new family.

Based on the small quadrats there is an average population of 9,822 per square meter (40,000,000 per acre). For the large quadrats the figures were 3,803 per square meter (15,500,000 per acre). The highest value for a small quadrat was 19,472 per square meter (79,000,000 per acre) and for a large one, 13,923 per square meter (56,000,000 per acre). These figures are based on the results for manual collection of all groups except the Acarina and Collembola which were collected by the Berlese funnel as explained in the text.

The biomass, based on 67 per cent of the animals, was 15.53 grams of animal protoplasm per square meter (138 pounds per acre).

An Eltonian pyramid of numbers, based on the small quadrats is presented.

The only factors in the soil analysis which varied significantly were pH and potassium. The number of animals present does not seem to be correlated with the potassium content of the soil. There is a suggestion,

especially in the small quadrats, that high population values are associated with a neutral pH. There is some correlation between soil moisture and population density.

Within certain limits the amount of leaf mold does not directly control the number of organisms, but very high and very low amounts do act as controlling factors.

Army ants were the only predator factor that could be correlated directly with the population density. In two cases where army ants had raided in an area on the day preceding collection, the population density was very low.

During the day there was no apparent correlation between time of collection and number of animals.

Two quadrats collected at night gave very low values for the population density. It may be that there is a nocturnal fluctuation in population due to migration into higher strata or into the soil.

There was a gradual increase in population density during the month of July. It is suggested that there is a seasonal change in population density with a low density in the dry season. Collections made early in the rainy season show a gradual rise in population correlated with the onset of the rains.

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